# 甘肃兰州盆地咸水河组下段红色 泥岩中的跳鼠化石<sup>1)</sup>

# 王伴月 邱占祥

(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要 兰州盆地咸水河组下段上部红色泥岩共产有4属8种跳鼠: Parasminthus asiae-centralis, P. tangingoli, P. parvulus, Parasminthus sp. 1, Parasminthus sp. 11, 黄河筒齿鼠(新属、种) Litodonomys huangheensis gen. et sp. nov., 兰州异 鰀鼠(新种) Heterosminthus lanzhouensis sp. nov. 和 Sinosminthus sp.。Litodonomys huangheensis 的主要特征是颊齿比例上较宽短,冠面结构较简单,脊较发育,下中脊短或无,下外脊直接由下原尖伸出。Heterosminthus lanzhouensis为 Heterosminthus属的一较原始的种。它的臼齿的颊、舌侧主齿尖虽错位,但幅度还较小,M1/2 具原小尖,但无原附尖,m1 具发达的下中脊,下外脊折线形,下外中脊向前倾等。

兰州盆地下红泥岩所产跳鼠组合基本上与甘肃省党河流域 Taben-buluk的一致。它们的时代可能大致相当, 为晚渐新世。

本文用 PAUP3.1.1 对早第三纪的各跳鼠属间的关系作了分析和讨论。

跳鼠在晚渐新世时在兰州盆地较繁盛,可能表明兰州盆地当时的气候已与现在我国的西 北地区的比较接近,为较干燥的温带草原和疏林干草原环境。

关键词 甘肃兰州盆地,咸水河组,晚渐新世,跳鼠科

中图法分类号 O915.873

# 兰州异蹶鼠 Heterosminthus lanzhouensis sp. nov.

(图 2; 图版 III, 1~8)

?Sicistinae indet., Bohlin, 1946, p. 53-54, fig.4: 5-7.

正型标本 左 m1 (IVPP V 11773.1)。

正型标本产地 兰州盆地上西沟 GL 9601B 地点。

归入标本 1M1(V 11772.1), 3 M2(V 11771.1~2, V 11772.2), 7 m1(V 11770.1, V 11771.3, V 11772.3~4, V 11773.2~4)和10 m2(V 11769.1~3, V 11770.2, V 11771.4和V 11773.5~9)。

产地 兰州盆地峡沟 GL 9513A (IVPP V 11769), GL 9513B (V 11770)和 GL

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9513C (V 11771)地点,上西沟 GL 9601A(V 11772)和 GL 9601B(V 11773)地点。

特征 大小与 Heterosminthus orientalis 相近,但较原始的异蹶鼠。颊齿比例上相对较短宽,舌、颊侧的主尖相对较少错位; MI/2 具原小尖和原尖后舌侧棱,但无明显的原附尖; m1 下外中脊通常向前颊侧斜,下外脊为折线; m2 具下中尖和下中脊。

#### 简齿鼠 Litodonomys gen. nov.

属型种 Litodonomys huangheensis sp. nov.

归入种 仅一种。

地理分布和地质时代 中国甘肃省,晚渐新世。

特征 中等大小的蹶鼠。颊齿比例上较宽短,主齿尖较压缩。ml~3下中脊很短,向前舌侧斜或缺失,下外脊由下原尖斜向后舌方伸达下次尖前臂。ml具明显下后附尖脊。m2 舌侧的四条横脊(前齿带舌部、下后脊、下次脊和下后边脊)均较发达,横向延伸,无下原尖后臂。m3下次脊与下后边脊融合。

**名称来源** Litodonomys = litos + odon + o + mys,希腊字: litos:简单, odon,牙齿, mys 鼠。意即此类鼠具较简单的颊齿结构。

# 黄河简齿鼠 Litodonomys huangheensis sp. nov.

(图版 III, 9~12)

aff. Eumys?, Bohlin 1946, p. 57, fig. 3: 61~63.

Eucricetodon, Lindsay, 1977, p. 602

正型标本 右 m2(IVPP V 11768.1)。

正型标本产出地点 兰州盆地上西沟 GL 9601B 地点。

**归入标本** 1m1(V 11768.2), 2 m2 (V 11767.1, V 11768.3)和4 m3 (V 11767.2~3, V 11768.4~5)。

地点 兰州盆地峡沟 GL 9513C (V 11767)地点和上西沟 GL 9601B (V 11768)地点。 特征 同属的特征。

名称来源 Huanghe. 黄河, 化石产地位于黄河流域。

比较与讨论 Bohlin (1946, p. 57, fig. 3: 61~63)在描述甘肃省党河地区塔奔布鲁克地点的化石时,认为其中的 2 枚 m2 (T.b. 211 和 T.b. 580)的形态,如牙齿比较宽短,下前凹较宽大,下后脊横向,在下后脊和下次脊之间只有短而向前舌侧斜的下中脊,缺下原尖后臂等特点与 Parasminthus 的不同。并指出,有的仓鼠如 Eumys 的 m2 牙齿比例上较宽,但党河的标本既缺下外中脊,也缺下原尖后臂。因此当时 Bohlin 将它们暂定为 aff. Eumys?。Lindsay (1977, p. 602)认为 Bohlin (1946)归入 Cricetodon 和 Eumys 的 4 枚单个牙齿很可能属 Eucricetodon。党河的这二个标本与兰州的上述标本在形态结构上是相同的,特别与V 11768.3 的相似,而且大小相近,应属同一种。但从兰州的 m1 特点,如缺下前边尖,下原尖和下后尖相对,大小相近,下后脊完全和下外脊的形状等特点看,它们显然不属于仓鼠类而应属跳鼠类。

与 Parasminthus, Plesiosminthus, Heosminthus, Sinosminthus 等属比较,甘肃的标本在下臼齿比例上较宽短,结构较简单,尖较压缩,脊较发育,下中脊短或无,在 ml 的下后脊比较高,具下后附尖脊,m2下后脊横向,下前凹开阔,下外脊由下原尖伸达下次尖前臂,m3

下次脊和下后边脊完全愈合的特点都与该4属的不同。它们与 Allosminthus 的区别在于具发达的横向的下后脊,缺下原尖后臂,以及下中脊前斜等。而它们与 Heterosminthus 和 Protalactaga 等的区别更明显。 Gobiosminthus 和 Shamosminthus 等 嚴鼠只已知上颊齿,无法比较,但兰州的颊齿的结构较简单的特征显然与此二属不匹配。显然它们可能代表不同于上述属的新属,我们称其为黄河简齿鼠: Litodonomys huangheensis。

早第三纪各跳鼠属间的相互关系 我们用 PAUP3.1.1 对亚洲早第三纪各跳鼠属间的相互关系作了分析和讨论。用 Branch 和Bound 方法搜寻表明 Heosminthus 和 Parasminthus 应为有效的属。搜索产生了同等的二个最简约的分支树(图 3)。跳鼠已知最早在中始新世早期已经出现。它们在中始新世早期或更早时从亚洲起源后即明显分化。Primisminthus 代表较原始的一支,其时代分布为中~晚始新世。Banyuesminthus 为与跳鼠其他已知的属对应的姐妹组。在中始新世早期以 Ulkenulastomys 为代表和中始新世中期以 cf. Sinosminthus sp. 为代表的二支与其他跳鼠的关系不清楚。在晚始新世的跳鼠属中Allosminthus 和 Sinosminthus 代表较早分出的旁支,Heosminthus 可能代表进化的主要支系,成为后期的跳鼠的姐妹组。从早渐新世到晚渐新世时这一支进一步分异。其中一分支进化为 Plesiosminthus,迁到欧洲,进而迁到北美洲。在亚洲,Parasminthus 分异为五支,一支为 Parasminthus 属,它可延续到早中新世;Gobiosminthus 和 Shamosminthus 代表两个旁支;第四支进化为 Heterosminthus— Lophocricetus等;第五支演化为 Protalactaga—Allactaga等。

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# DIPODIDAE (RODENTIA, MAMMALIA) FROM THE LOWER MEMBER OF XIANSHUIHE FORMATION IN LANZHOU BASIN, GANSU, CHINA

WANG Ban-Yue QIU Zhan-Xiang

(Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044)

Abstract The dipodid fossils from the red mudstone of the Lower Member of the Xianshuihe Formation include eight species of four genera: Parasminthus asiae-centralis, P. tangingoli, P. parvulus, Parasminthus sp. I, Parasminthus sp. II, Litodontomys huangheensis gen. et sp. nov., Heterosminthus lanzhouensis sp. nov., and Sinosminthus sp. The new genus Litodontomys can be diagnosed as: having proportionally wider and shorter cheek teeth, with simpler occlusal pattern, well developed lophids, mesolophid short or absent, ectolophid extending from protoconid. The new species Heterosminthus lanzhouensis represents a primitive species of Heterosminthus. The main cusps of its molars are slightly alternate in position. The protoconule is distinct but the anterostyle is

absent on M1/2. m1 has developed mesolophid, bending ectolophid, and antero-buccally oblique ectomesolophid.

The dipodids described above are similar to those of Taben-buluk in composition. The middle part of the lower red mudstone bearing the dipodids may be equivalent to that of the latter in age. It is of late Oligocene.

The phylogenetic relationships of the Paleogene dipodids are analyzed based on dental features using PAUP 3.1.1.

The predominance of the dipodids in the late Oligocene micromammals in the Lanzhou Basin indicates that a grassland or savanna habitat might have been established in the Lanzhou area during that time.

Key words Lanzhou Basin of Gansu, Xianshuihe Formation, Late Oligocene, Dipodidae

The Xianshuihe Formation erected by C. C. Young and M. N. Bien (1937) as of middle Miocene in age has been comprehensively restudied and redefined (Qiu et al., 1997). Now it is subdivided into three members: the Lower Member is composed of the basal yellow sandstone and the overlying red mudstone (called as lower red mudstone); the Middle Member is composed of layers of white sandstone in the lower part and red mudstone in the upper part (called as upper red mudstone); the Upper Member is composed of interbedded sandstone, siltstone and mudstone. The white sandstone (Middle Member) and the yellow sandstone (basal Lower Member) were recognized as of early Miocene and Oligocene respectively (Qiu, 1989, Qiu et Qiu, 1990, 1995 Qiu et al., 1997). Since then the age of the intercalated lower red mudstone becomes one of the focal problems: Is it of Oligocene or Miocene?

Oiu et Gu (1988) reported some micromammal fossils from red beds at the northern slope of the Gaolan mountain of the Lanzhou Basin. However, this locality is located at the south bank of the Yellow River. Its relationship with the red mudstone widely distributed on the north bank of the Yellow River is obscure. No fossils had been discovered in the lower red mudstone on the north bank of the Yellow River until 1995. Since then more and more mammal fossils including micromammals were collected from the lower red mudstone in Xiagou, Shangxigou and Qujiachuan. These discoveries are significant not only for understanding the mammalian fauna, but also for determining the age of the lower red mudstone. The Dipodidae, which are the most abundant in quantity and the most diverse in taxon, are described in this paper.

The terms used in this paper mainly follow Wang (1985). In the description the frequency of a character variant is expressed as a fraction, with the numerator indicating the number of the variant and the denominator the total number of the specimens examined. Thus, 8/14 indicates that out of 14 specimens 8 belong to the

variant described.

Abbreviations for the repositories or localities are: GL. locality of the Gansu Provincial Museum; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; T. b., Taben-buluk, Gansu, China; UTL. Ulantatal area, Nei Mongol, China. The measurements of the dentition utilize the positional abbreviations: L, length; W, width.

# 1 Systematics

# Dipodidae Fischer de Waldheim, 1817 Parasminthus Bohlin, 1946 Parasminthus asiae-centralis Bohlin, 1946

(fig.1; pl. 1, 9~14; pl. II, 7)

Parasminthus asiae-centralis Bohlin, 1946 (partim): pp. 18~22.

Specimens Two P4 (IVPP V 11749.1, V 11750.1), 3 M1 (V 11750.2, V 11752.1~2), 2 M2 (V 11750.3, V 11752.3), 6 mI (V 11748.1~3, V 11749.2~3, V 11750.4), 7 m2 (V 11748.4, V 11750.5~6, V 11751.1~3, V 11752.4) and 3 m3 (V 11749.4~5, V 11751.4).

Localities and horizons GL 9513A (IVPP V 11748), GL 9513B (V 11749), GL 9513C (V 11750) in Xiagou, and GL 9601A (V 11751) and GL 9601B (V 11752) in Shangxigou, Lanzhou Basin, Gansu, China; late Oligocene, the middle part of the red mudstone of the Lower Member of the Xianshuihe Formation

**Emended diagnosis** Large-sized *Parasminthus*. P4 composed of a main cusp and a posterior cingulum, M1/2 with posterior concavity between hypocone and posteroloph, metaloph of M1 joining posteroloph, M2 with double protoloph, anteroconid usually isolated on ml.

**Remarks** The specimens are identical with those of P. asiae-centralis in size, having four roots and a posterior concavity between hypocone and posteroloph on  $M1 \sim 2$ , M1 having a metaloph joining the posteroloph, M2 having double protoloph, and m1 with isolated anteroconid.

**Measurements** (L × W) P4:  $0.8 \times -$ ,  $0.75 \times 0.75$ ; M1:  $1.75 \times 1.55$ ,  $1.77 \times 1.5$ ,  $2.05 \times 1.75$ ; M2:  $1.7 \times -$ ; m1:  $1.75 \times 1.35$ ,  $1.7 \times 1.2$ ,  $1.7 \times 1.16$ ; m2:  $1.7 \times 1.25$ ,  $1.65 \times 1.35$ ,  $1.75 \times 1.3$ ; m3:  $1.6 \times 1.35$ ,  $- \times 1.3$ .

Huang (1992) revised the diagnosis of *P. asiae-centralis* based on the specimens from Ulantatal area, Alxa Zuoqi, Nei Mongol, China. Having compared the specimens from Taben-buluk, Lanzhou and Ulantatal, we found that the specimens from Taben-buluk and Lanzhou were more similar to each other, and different from those of the Ulantatal area in some features. These distinctive characters of the Ulantatal

specimens, as mentioned by Huang (1992) in his revised diagnosis, seem to us to be primitive ones. In view of the fact that the Ulantatal fauna is of late early Oligocene, older than that of Taben-buluk, the Ulantatal specimens might represent a more primitive stage than the typical *P. asiae-centralis*. Huang's revised diagnosis seems to be applicable only to the Ulantatal specimens, not to the specimens from the type area, Taben-buluk, and Lanzhou.

# Parasminthus tangingoli Bohlin, 1946

(fig. 1; pl I,  $1 \sim 8$ )

Parasminthus asiae-centralis Bohlin, 1946 (partim): pp. 18~22, fig. 3: 29

Parasminthus asiae-centralis Huang, 1992 (partim): pp. 250~255, 275~277

Parasminthus tangingoli Huang, 1992 (partim): pp. 255~260, 277~279

Parasminthus parvulus Huang, 1992 (partim): pp. 260~265, 279~281

**Specimens** One fragment of lower jaw with m1 $\sim$  2 (IVPP V 11755.10), 3 P4 (V11753.1 $\sim$  2, V 11755.1), 12 M1 (V 11753.3, V 11754.1 $\sim$  3, V 11755.2 $\sim$  3, V 11756.1, V 11757.1 $\sim$  5), 21 M2 (V 11753.4 $\sim$  7, V 11755.4 $\sim$  7, V 11756.2 $\sim$  6, V 11757.6 $\sim$  13), 13 M3 (V 11753.8 $\sim$  9, V 11754.4 $\sim$  7, V 11755.8 $\sim$  9, V 11756.7, V 11757.14 $\sim$  17), 23 m1 (V 11753.10, V 11754.8 $\sim$  13, V 11755.11 $\sim$  14, V 11756.8 $\sim$  10, V 11757.18 $\sim$  26), 24 m2 (V 11753.11 $\sim$  13, V 11754.14 $\sim$  15, V 11755.15, V 11756.11 $\sim$  13, V 11757.27 $\sim$  41) and 9 m3 (V 11753.14 $\sim$  15, V 11754.16 $\sim$  18, V 11756.14 $\sim$  15, V 11757.42 $\sim$  43).

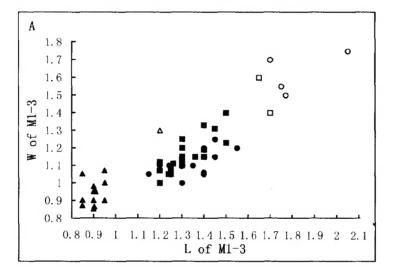
Localities and horizons GL 9513A (IVPP V 11753), GL 9513B (V 11754), GL 9513C (V 11755) in Xiagou, and GL 9601A (V 11756) and GL 9601B(V 11757) in Shangxigou, Lanzhou Basin, Gansu, Chinai late Oligocene, the middle part of the red mudstone of the Lower Member of the Xianshuihe Formation.

**Emended diagnosis** Medium-sized *Parasminthus*. P4 composed of main cusp and posterior cingulum, M1/2 with concavity between hypocone and posteroloph, metaloph joining posteroloph or posterior arm of hypocone on M1, M2 with double protoloph, anteroconid joining with metaconid or / and protoconid on ml.

**Remarks** P4 is composed of a main cusp and a posterior cingulum. M1 / 2 has a posterior concavity between hypocone and posteroloph and four roots. On M1 metaloph joins posteroloph or posterior arm of hypocone. M2 has double protoloph. m1 has an anteroconid joining metaconid and / or protoconid. All these features are identical with those of *P. tangingoli*. In addition, the size is within the range of variation of *P. tangingoli* (see table 1).

While describing *P. asiae-centralis* and *P. tangingoli*, Bohlin (1946) mentioned that they were almost indistinguishable except size. This made him rather hesitated in dealing with the specimens intermediate in size (T. b. 569a and 588). Huang (1992)

took the length of two anterior molars (1.5 mm) as the boundary line between *P. asiae-centralis* and *P. tangingoli*. Thus, according to him, the specimens with the M1 or M2 longer than 1.5 mm is assigned to *P. asiae-centralis* and those within the range from 1 mm to 1.5 mm to *P. tangingoli*. Our study of the Lanzhou material came to the same major conclusion as Bohlin and Huang did. There are little morphological differences between the two species. Some minor differences can be observed in the degree of the connection of anteroconid with protoconid or metaconid on m1. However, the size difference is significant. Our statistical analysis is



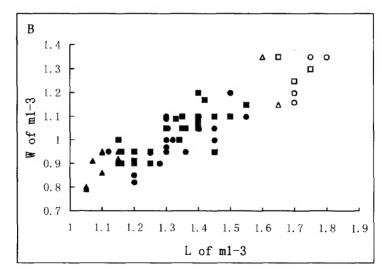


Fig.1 Diagram showing the size variation of molars of *Parasminthus asiae-centralis* and *P. tangingoli*, after the measurements of molars from Taben-buluk by Bohlin, 1946, and Lanzhou Basin

\*P. asiae-centralis: O M1/m1, □M2/m2, △M3/m3; \*P. tangingoli:

• M1/m1, ■ M2/m2, △M3/m3

supportive for the above conclusion as well. The coefficient of variation (CV) of the cheek teeth of the two species is too large to assign them all into one species. However, according to the diagram of the cheek teeth, a hiatus can be located around 1.6 mm between *P. asiae-centralis* and *P. tangingoli*, instead of 1.5 mm as suggested by Huang (fig. 1). According to this criterion, some of the Ulantatal specimens referred to *P. asiae-centralis* and the specimen T. b. 569a, which was hesitatingly referred by Bohlin (1946) to *P. asiae-centralis*, should be referred to *P. tangingoli*.

Bohlin's diagnosis of *P. tangingoli* (1946) was based on the following features: the metaloph joining the posterior arm of hypocone or the posteroloph on M1; M2 having double protoloph; and M1/2 having four roots. Huang (1992) revised diagnosis of *P. tangingoli* based on the specimens from the Ulantatal area. The Lanzhou specimens referred to *P. tangingoli* are in complete agreement with Bohlin's diagnosis of this species, but quite different from that of Huang. It seems more probable that the Ulantatal specimens are in a transitional stage from a more primitive form to the typical *P. tangingoli* and represent *P.* aff. *P. tangingoli*. It is inadvisable to change the diagnosis of *P. tangingoli* based on the Ulantatal specimens.

Table	1 (	vicasurements (	of cheek	teeth of	Parasminthus	tangingoli	Bohlin, 1946	(mm)	
			- 54						7

		N	Min	Max	Aver	SD	CV
D4	L	3	0.6	0.7	0.65	0.04	6.29
P4	W	3	0.6	0.7	0.67	0.05	7.07
Ml	L	9	1.2	1.55	1.4	0.09	6.3
1411	W	9	1	1.25	1.13	0.08	7.1
M2	L	21	1.15	1.5	1.3	0.1	7.3
1712	W	20	1.05	1.4	1.16	0.1	8.47
M3	L	13	0.8	0.95	0.89	0.04	5.01
IVIS	W	11	0.85	1.07	0.94	0.07	7.77
ml	L	16	1.12	1.55	1.34	0.11	8.49
1111	W	24	0.82	1.2	0.97	0.09	9.47
m2	L	24	1.15	1.55	1.31	0.12	8.88
mz	W	31	0.85	1.28	1.01	1.1	10.27
m3	L	7	1.05	1.1	1.1	0.03	3.13
щэ	W	7	0.8	0.95	0.91	0.05	5.81

<sup>\*</sup> L: length; W: width; N: number of specimens; Min: minimum; Max: maximum; Aver: average; SD: standard deviation; CV: coefficient of variation

#### Parasminthus parvulus Bohlin, 1946

(pl II, 1~4)

Parasminthus parvulus Bohlin, 1946: pp. 30~41

Parasminthus tangingoli Huang, 1992 (partim): pp. 255~260, 277~279

Parasminthus parvulus Huang, 1992 (partim): pp. 260~265, 279~281

**Specimens** Six fragments of maxillaries (IVPP V 11758.1~3, V 11759.1~2, V 11762.1), 5 fragments of lower jaws (V 11758.74~76, V 11759.66~67), 15 P4 (V 11758.4, V 11759.3, V 11760.1, V 11761.1, V 11762.2~12), 126 M1 (V 11758.5~39, V 11759.4~32, V 11760.2~11, V 11761.2~12, V 11762.12~53), 100 M2 (V 11758.40~72, V 11759.33~56, V 11760.12~22, V 11761.13~21, V 11762.54~76), 16 M3 (V 11758.73, V 11759.57~65, V 11760.23~25, V 11761.22, V 11762.77~78), 78 m1 (V 11758.77~107, V 11759.68~84, V 11760.26~29, V 11761.23~27, V 11762.79~99), 86 m2 (V 11758.108~126, V 11759.85~101, V 11760.30~40, V11761.28~36, V 11762.100~129), and 43 m3 (V 11758.127~139, V 11759.102~108, V11760.41~43, V 11761.37, V 11762.130~148).

Localities and horizons GL 9513A (IVPP V 11758), GL 9513B (V 11759) and GL 9513C (V 11760) in Xiagou, and GL 9601A (V 11761) and GL 9513B (V 11762)in Shangxigou, Lanzhou Basin, Gansu, China; late Oligocene, the middle part of the red mudstone of the Lower Member of Xianshuihe Formation.

Emended diagnosis Small-sized *Parasminthus*. P4 usually E shaped in occlusal pattern, M1~2 lacking a posterior concavity between hypocone and posteroloph, on M1 metaloph joining with hypocone, M2 having single protoloph, on m1 anteroconid present or absent.

**Remarks** The specimens from Lanzhou Basin are identical with *P. parvulus* in occlusal pattern: M1/2 lacking concavity between hypocone and posteroloph and having 4 roots, on M1 metaloph joining with hypocone, M2 with single protoloph. They are similarly small in size.

In his revised diagnosis of P. parvulus Huang (1992) mentioned some distinct features in occlusal pattern. However, his separation of P. parvulus from P. tangingoli was mainly based on size difference. He took 1 mm of the length of M1/2 as the boundary line between P. tangingoli and P. parvulus. The specimens with the M1/2 longer than 1mm are referred to P. tangingoli and those shorter than 1mm to P. parvulus, regardless of morphological features. This makes it difficult to distinguish the two species in practice. Huang (1992) referred two M1 (IVPP V 10160.39 and V 10160.221) to P. parvulus based on size, but he mentioned that the two M1 had the feature of P. tangingoli: metaloph joining the posteroloph. As pointed out by Bohlin (1946), P. parvulus is different from P. tangingoli mainly in morphological features, not in size. In fact, he referred some M1 and M2, which is over 1mm in length, to The Lanzhou specimens tend to prove this conclusion. distinguish P. parvulus from P. tangingoli morphologically. However, the two species may overlap in size. There are specimens with characteristic features of P. tangingoli, but their M1/2 are shorter than 1mm, while some others with definite features of P. parvulus, but their M1/2 longer than 1mm. Thus, some of the Ulantatal specimens originally referred to *P. tangingoli* by Huang based purely on the size may belong to *P. parvulus*, and some others referred to *P. parvulus* by Huang (1992) may belong to *P. tangingoli*.

All the MI/2 from Taben-buluk and Lanzhou referred to *P. parvulus* have 4 roots. However, the number of the roots of M1/2 from the Ulantatal area referred to *P. parvulus* by Huang (1992) varies from 3 to 4 roots. As mentioned in the paragraph of *P. tangingoli*, the Ulantatal fauna is older than that of Taben-buluk and the specimens of *P. parvulus* from the Ulantatal area may represent a more primitive stage than the typical *P. parvulus*.

Table 2 Measurements of Payagninthus napulus Doblin 1046

		Table 2	Measurements of	Parasminthus	parvulus Bon	lin, 1946	(mm)
		N	Min	Max	Aver	SD	CV
	Ĺ	16	0.45	0.62	0.55	0.05	8.46
P4	w	16	0.45	0.68	0.57	0.06	9.9
Ml	L	109	0.75	1.25	1.04	0.09	8.35
1411	w	109	0.75	1.13	0.95	0.08	8.31
M2	L	86	0.76	1.12	0.94	0.07	7.56
IVIZ	w	86	0.7	1.05	0.88	0.07	7.9
M3	L	14	0.56	0.75	0.66	0.05	7.83
1013	w	14	0.65	0.8	0.73	0.05	6.82
ml	L	67	0.9	1.15	1.04	0.06	5.76
1111	w	67	0.67	0.88	0.79	0.06	7.18
m2	L	60	0.85	1.15	1.03	0.07	6.62
1112	w	60	0.7	0.95	0.82	0.05	6.37
m3	L	39	0.7	0.95	0.84	0.06	7.16
1112)	w	39	0.65	0.87	0.75	0.05	6.44

<sup>\*</sup> The terms used here are similar to those in table 1.

#### Parasminthus sp. I

(pl. II, 8)

Four m2 (IVPP V 11763.1~2, V11764, V 11765) were collected from GL 9513A (V 11763) in Xiagou and GL 9601A (V 11764) and GL 9601B (V 11765) in Shangxigou of Lanzhou Basin, Gansu, China. They are larger than *P. asiae-centralis* (L×W: 1.95×1.45; 2.15×1.56; 2.35×1.6). The cheek tooth crown is higher. The metaconid and entoconid shift slightly more anteriorly than protoconid and hypoconid. The short metalophid I is oblique antero-buccally, joining anteroconid. The anterior arm of protoconid is weak or absent. The developed posterior arm of the protoconid meets the mesostylid. The hypolophid is transverse. The lingual part of anterior cingulum and anterior fossettid are reduced. The anteroconid and buccal part of anterior cingulum are developed. The anterior sinusid is large. The mesoconid is

distinct. The ectomesolophid is more or less present. They are similar to that of *Parasminthus* in the basic features of the cheek teeth. However, they are larger than all the known species of *Parasminthus*, including *P. asiae centralis*. In addition, they have higher tooth crown, more anteriorly located metaconid and entoconid, a lower and weaker lingual part of the anterior cingulum and a reduced anterior fossettid. They may represent a larger and more advanced species than *P. asiae-centralis*.

#### Parasminthus sp. II

(pl. II, 6)

Two M1 (IVPP V 11766.1~2) from GL 9513C in the Xiagou of Lanzhou Basin are similar to P. tangingoli in having a complete mesoloph, an obliquely positioned metaloph joining with posteroloph and in size (L × W:  $1.5 \times 1.3$ ,  $- \times 1.4$ ). However, they are different from P. tangingoli and other species of Parasminthus, and Gobiosminthus in having an antero-posteriorly compressed protocone, without posterior arm, a short protoloph joining anterior arm of protocone, short anterior fossette and anterior middle fossette, and a deeper anterior part of sinus. They may represent a new species of Parasminthus.

# Heterosminthus lanzhouensis sp. nov.

(fig. 2; pl. III,  $1 \sim 8$ )

?Sicistinae indet., Bohlin, 1946: pp. 53~54, figs 4: 5~7.

Cricetidae, Lindsay, 1977: p.602.

Holotype A left m1 (IVPP V 11773.1).

Locality and horizon of holotype GL 9601B in Shangxigou of Lanzhou Basin; late Oligocene, the middle part of the upper red mudstone of the Lower Member of the Xianshuihe Formation.

**Referred specimens** One M1 (IVPP V 11772.1), 3 M2 (V 11771.1 $\sim$  2, V 11772.2), 7 m1 (V 11770.1, V 11771.3, V 11772.3 $\sim$  4, V 11773.2 $\sim$  4) and 10 m2 (V 11769.1 $\sim$  3, V 11770.2, V 11771.4, V 11773.5 $\sim$  9).

Localities and horizons GL 9513A (V 11769), GL 9513B (V 11770) and GL 9513C (V 11771) in Xiagou, and GL 9601A (V 11772) and GL 9601B (V 11773) in Shangxigou of Lanzhou Basin, Gansu, China; late Oligocene, the middle part of the upper red mudstone of the Lower Member of the Xianshuihe Formation.

**Diagnosis** Close to *Heterosminthus orientalis* in size but more primitive; cheek teeth proportionally shorter and wider, with slightly alternated main cusps; on M1/2 protoconule distinct, protocone with posterolingual crest but without anterostyle; m1 with developed, usually antero-buccally oblique ectomesolophid, bending ectolophid; m2 with mesolophid.

Etymology Lanzhou Basin is the area where the fossils were collected.

**Description** All the specimens are isolated teeth. The cheek teeth are brachydont

with distinct main cusps and lower lophs.

Ml is rectangular in occlusal view, and longer than wide. Four main cusps are distinct and subequal in size, but the lophs connecting the main cusps are low and slender. The protocone and hypocone shift slightly more anteriorly than the paracone and metacone. The anterior arm of the protocone extends antero-buccally, but does not meet the parastyle. The distinct protoconule is close to the protocone on its anterior arm in the position. The protocone has a distinct postero-lingual crest, but does not have distinct cusp on this crest. This cusp was called as anterostyle (Qiu, 1985, fig. 1). The protoloph and metaloph extend postero-lingually to meet the entoloph and posteroloph respectively. At the point where the metaloph and posteroloph link up there is a distinct cusp, which is called as posterocone here. The mesoloph is complete, extending from the distinct mesocone to the mesostyle. The entoloph is complete and slightly concave lingually, with a slightly lower anterior end. There is a gap between the posterior arm of the hypocone and the short posteroloph. The anterior cingulum is developed and extends along the anterior side of the tooth. The parastyle is distinct. The posteroloph is short. The short lingual part of the posterior cingulum is distinct. The wide sinus is slightly oblique antero-buccally and opposite to the anterior fossette. The posterior sinus is small but distinct. M1 has 4 roots.

M2 is rectangular in occlusal view, with a straight and wider anterior side. The protocone shifts slightly more anteriorly than the paracone. The two cusps are subequal in size. Like in M1 the anterior arm of the protocone does not meet the paracone to form the protoloph I, but extends antero-buccally. It may be free (1/3) or may link with the anterior cingulum (2/3). The developed protoconule is close to the protocone in the position. The postero-lingual crest of the protocone is weak. A weak postero-external crest of paracone is present. The short protoloph extends from the paracone to the entoloph. The mesoloph connects the mesocone with the mesostyle. The metacone is the smallest among the main cusps. The metaloph extends anterolingually to meet the anteiror arm of the hypocone or the entoloph. The hypocone is smaller than the protocone but larger than the metacone in size and opposite to the metacone in the position. The posterior arm of the hypocone links with the posteroloph. The more or less distinct posterocone is separated from the hypocone by a shallow groove. The entoloph is complete. The developed anterior cingulum is divided into buccal and lingual parts by the distinct anterocone. The anterocone is connected with the protoconule by a short crest. The wide sinus extends antero-buccally and opposite to the anterior fossette. The anterior sinus is narrow and shallow. M2 has 4 roots.

ml is oval in occlusal view, and with narrower and anteriorly convex anterior

border. The protoconid and metacone are subequal in size but the former is slightly more posteriorly located than the latter. The lower, slender and oblique posterior arms of both cuspids meet together to form a V-shaped metalophid II. The developed anteroconid may have one or two accessory crests to meet the metacone (1/8) or both the metacone and the protocone (4/8), or may have not any accessory crest (3/8). The entoconid and hypoconid are higher and larger than the anterior two ones. Among them the hypoconid is the larger and slightly more posteriorly positioned than the entoconid. The anterior arm of the hypoconid is short and low. The mesoconid is always distinct and usually smaller than the anteroconid. One of the particular features is the ectolophid. It is curved rather than straight. The posterior part behind the mesoconid is longitudinal, but the middle part anterior to the mesoconid turns antero-lingually, and then the anterior part turns anteriorly to meet the top of the V-shaped metallophid II. A gap is usually present between the posterior end of the ectolophid and the anterior arm of the hypoconid. The mesolophid ( = posterior arm of the protoconid of Oiu, 1996) extends from the turning point of the anterior and middle parts of the ectolophid rather than from the mesoconid. It may reach the metastylid or mesostylid (6/7) or may be free (1/7). The mesostyle is more or less distinct. The developed ectomesolophid is usually oblique antero-buccally (7/8) and may meet the protoconid (4/7) or may be free (3/7). In V11771.3 the ectomesolophid is transverse and an accessory oblique crest extends from the mesoconid to the posterior arm of the protoconid. The specimen is similar to T. b. 592c from Taben-buluk described by Bohlin (1946, pp.  $53 \sim 54$ , fig. 4:  $5 \sim 7$ ). The short and transverse hypolophid may join the mesoconid (4/8) or the ectolophid behind the mesoconid (4/8). The posterolophid connects the hypoconid with the entoconid. The hypoconulid is separated from the hypoconid by a distinct posterior sinusid. posterior cingulum extends from the hypoconulid to the buccal border. The sinusid is large, m1 has a small anterior root and a large posterior one.

m2 is rectangular in occlusal view, and longer than wide. The four main cusps are distinct. The protoconid and hypoconid shift slightly posteriorly than the metaconid and entoconid. The metaconid is subequal to the protoconid in size and close to the anterior cingulum in the positon. The short metalophid I is oblique anterobuccally and joins the distinct anteroconid. The anterior cingulum is divided into a low and short lingual part and a developed buccal one. The short and lower anterior arm of the protoconid connects the anteroconid. The developed posterior arm of the protoconid may join the metastylid (6/10) or the posterior wall of the metaconid (4/10). The hypoconid is the largest and the entoconid the smallest. The hypolophid is transverse or slightly oblique antero-buccally to meet the mesoconid or the ectolophid behind it. The short ectolophid extends obliquely to the posterior wall of the protoconid. The

mesoconid is more or less present. The mesolophid may be absent (4/10) or short and oblique antero-buccally (6/10) to meet or not the posterior arm of the protoconid. No distinct ectomesolophid can be seen. The posterolophid extends from the hypoconid to the entoconid. The hypoconulid is separated from the hypoconid by a more or less distinct posterior groove. The anterior fossettid is very small and shallow. The crescent trigonid basin communicates with the anterior sinusid, forming a S-shaped groove. The middle sinusid is wide. The anterior sinusid is large, but the posterior sinusid is vestigial. m2 has two roots.

Measurements See table 3.

Table 3	Measurements	of chee	k teeth	of	Heterosminthus	lanzhouensis	sp. nov.	(mm)
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		Z	Min	Max	Aver	SD	CV
MI	L	1			1.38		
1711	W	1			1.15		
M2	L	3	1.26	1.4	1.32	0.059	4.46
IVIZ	w	3	1.05	1.2	1.12	0.062	5.58
1	L	8	1.3	1.55	1.41	0.085	6
m1	w	8	0.91	1.16	1.05	0.068	6.46
7	L	8	1.2	1.45	1.37	0.072	5 27
m2	w	8	0.9	1.1	1.03	0.076	7.44

<sup>\*</sup> The terms used here are similar to those of table 1.

Comparison and discussion The cheek teeth of the Lanzhou specimens are similar to those of Heterosminthus in being proportionally narrow and long, having alternating main cusps, and slender lophs, M1/2 having a postero-lingual crest, M1 having a distinct lingual part of the posterior cingulum, a distinct posterior sinus, and a weak entoloph, M2 having single protoloph II, an anterior arm of protocone extending antero-buccally not joining the paracone, m1 having a V shaped metalophid II joining the anterior part of bending ectolophid, m2 having an anterior shifting metaconid, a short metalophid joining anteroconid, a well developed buccal part of the anterior cingulum, a large anterior sinusid, a developed posterior arm of the protoconid joining the metaconid and an oblique ectolophid. Thus they are referred to Heterosminthus. Of this genus only one species, H. orientalis, is known from middle Miocene of China (Schaub, 1930; Qiu, 1996). The differences of the Lanzhou specimens from these of H. orientalis are as follows: the cheek teeth are proportionally wider and shorter, M1 and M2 lack distinct anterostyle, m1 has a curved ectolophid, and an antero-buccally oblique ectomesolophid, and m2 has a mesolophid. These features are primitive ones. The Lanzhou specimens seem to represent a more primitive species than H. orientalis. It is here named H. lanzhouensis.

Bohlin (1946, pp.  $53 \sim 54$ , fig. 4:  $5 \sim 7$ ) described a m1 (T. b. 592c) from

Taben-buluk as ? Sicistinae sp. Lindsay (1977, p. 602) suggested that T. b. 592c was more closely related to either *Eucricetodon* or *Pseudocricetodon*, and should be assigned to the Cricetidae. As described above, T. b. 592c is in fact similar to that of *H. lanzhouensis*, especially to V11771.3. Its size also falls within the range of variation of this species. Thus, T. b. 592c is to be referred to *H. lanzhouensis*.

Having compared H. lanzhouensis with Parasminthus and H. orientalis, we found it possible that the evolution of the cheek teeth may proceed from *Parasminthus* to Heterosminthus. The evolutionary trend would include: the change of the cheek teeth from shorter and wider into longer and narrower and the arrangement of the main cusps from opposite to alternative. During this process other elements of the cheek teeth also change. The anterior fossette of the upper molars is enlarged; the postero-lingual crest of the protocone develops; the anterior arm of the protocone of M2 extends anteriorly; on the lower molars the anterior fossettid is reduced and the anterior sinusid enlarged. It is interesting to point out the change of the ectolophid and mesolophid on m1 (fig. 2). In Parasminthus the ectolophid is straight and usually joins the protoconid, and the mesolophid extends from the mesoconid to the mesostylid. In H. lunzhouensis the ectolophid is curved. Probably its anterior part before the mesoconid is composed of part of the original mesolophid. When it shifts anteriorly the mesolophid may meet the top of the V-shaped metalophid II at its middle. Thus, the original mesolophid may be subdivided into two parts: the buccal part may form the anterior part of the ectolophid; the lingual part may remain as the short mesolophid. Therefore, the mesolophid in *Heterosminthus* does not join the mesoconid, but is separated from the latter by a short distance. This distance may be the buccal part of the original mesolophid or the anterior part of the recent ectolophid. At the same time the anterior part of the original ectolophid of Parasminthus shifts postero-buccally so that it becomes the ectomesolophid. This supports Bohlin (1946, p. 53) in that the oblique crest from the mesoconid in T. b. 592c might be the vestige of the ectolophid. With the lingual part of the teeth shifting more anteriorly from H. lanzhouensis to H. orientalis, the ectolophid changes from being curved to straight, but the oblique antero-lingually ectomesolophid from being oblique to transverse. In m2 of Parasminthus the long middle transverse lophid in the middle fossettid, which may be formed by a mesolophid from the mesoconid or by the posterior arm of the protoconid, always joins the mesoconid. In m2 of H. lanzhouensis the posterior arm of the protoconid joins metastylid or metaconid and the mesolophid remains, while in orientalis the posterior arm of the protoconid joins the metaconid and the mesolophid is lost. Obviously *H*. lanzhouensis is in the transitional stage from Н. orientalis. Probably Heterosminthus derives from to Parasminthus species with long posterior arm of the protoconid. This supports Qiu's hypothesis (Qiu et al., 1981 and Qiu, 1996). However, Heterosminthus is more similar to P. tangingoli in such features as M1/2 with concavity between the hypocone and the posteroloph, M1 having metaloph joining the posteroloph, and M2 having double protolophs. Probably Heterosminthus derived from some form near P. tangingoli.

# Litodonomys gen. nov.

**Type species** Litodonomys huangheensis sp. nov.

Referred species Only one species.

Geographic distribution and geological range Gansu, China; late Oligocene.

Medium-sized dipodid; cheek teeth Diagnosis proportionally wide and short, with simple occlusal pattern and compressed main cusps; on lower molars posterior arm of protoconid absent. mesolophid short and oblique antero buccally ectolophid obliquely extending protoconid to anterior arm of hypoconid; m1 with distinct metastylid; m2 with only four transverse lingual lophids; m3 reduced with fused hypolophid and posterolophid.

**Etymology** Litodonomys = litos + odon + o + mys. Greek: litos: simple, odon: tooth, mys: mouse. It implies that the occlusal pattern of the cheek teeth is simple.

#### Litodonomys huangheensis sp. nov.

(pl. III,  $9 \sim 12$ )

aff. Eunys?, Bohlin, 1946: p. 57, fig.3: 61~63.

Eucricetodon, Lindsay, 1977: p. 602.

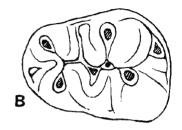
Holotype One right m2 (IVPP V 11768.1).

Localities and horizon of holotype GL 9601B in Shangxigou of Lanzhou Basin; late Oligocene, the middle part of the upper red mudstone of the Lower Member of the Xianshuihe Formation.

**Referred speciemns** One m1 (V 11768.2), 2 m2 (V 11767.1, V 11768.3) and 4 m3 (V  $11767.2 \sim 3$ , V  $11768.4 \sim 5$ ).

Localities and horizon GL 9513C (V 11767) in Xiagou and GL 9601B (V







#### 1 m m

Fig. 2 Comparison of occlusal view of ml of *Parasminthus tangingoli*, *Heterosminthus orientalis* and *H. lanzhouensis* sp. nov.

A. Parasminthus tangingoli (T. b. 590n, after Bohlin, 1946, fig. 3: 34), B. Heterosminthus lanzhouensis sp. nov. (V 11773.1, holotype), C. H. orientalis (V 10368.309, after Qiu, 1996, fig. 42E)

11768) in Shangxigou of Lanzhou Basin; late Oligocene, the middle part of the red mudstone of the Lower Member of the Xianshuihe Formation.

Diagnosis Same as the genus.

**Etymology** Huanghe, the second largest river in China. The fossils were collected from the Huanghe River valley.

**Description** m1 is trapezoidal in occlusal view. The anteroconid is absent. The protoconid and metaconid are subequal in size and opposite to each other in position. The metalophid II is complete. The trigonid basin opens anteriorly. The metastylid is distinct. The mesolophid is weak, short and oblique antero buccally. The compressed hypoconid extends antero buccally. The ectolophid extends from the protoconid to the anterior arm of the hypoconid. The wide sinusid is oblique postero-lingually.

m2 is nearly rectangular in occlusal view, and longer than wide. The four main cusps are compressed. The protoconid may be equal to or larger than the metaconid. The anterior arm of the protoconid extends to the anterior cingulum and separates it into two parts. The metastylid is more or less present. Four transverse lophids are developed. The transverse metalophid and hypolophid meet the anterior arms of the protoconid and hypoconid respectively. No posterior arm of protoconid is visible. The entoconid and metaconid are subequal in size and close to each other in position. The hypoconid is the largest. The ectolophid is similar to that in m1, which obliqually extends from the protoconid to the anterior arm of the hypoconid. The mesolophid may be very short and oblique antero buccally (1/3) or absent (2/3). The posterolophid joins the hypoconid with the entoconid to close the large posterior fossettid. The anterior fossettid is wide and transverse, but shorter than the posterior one. The middle fossettid is the largest and has a narrow exit. The anterior sinusid is wider than the anterior fossettid. The sinusid is large and oblique postero-lingually, m2  $(L \times M)$ :  $1.45 \times 1.15$ ,  $- \times 1.25$ ,  $1.1 \times 1.08$ .

m3 is triangular with round angles. The anterior part of m3 is similar to that of m2. But the posterior part is well reduced. The ectolophid is short, extending from the protoconid to the posterolophid. No mesolophid can be seen. The entoconid is the smallest and the hypoconid is much smaller than the anterior two main cusps. The hypolophid and posterolophid are usually fused into one lophid and the posterior fossettid disappears (3/4). In V 11767.3 a vestige of the posterior fossettid surrounded by the short hypolophid and posterolophid can be seen. m3  $(L \times W)$ :  $1.25 \times 1.19$ ,  $1.2 \times 1.07$ ,  $0.95 \times 0.9$ .

**Comparison and discussion** Bohlin (1946) discribed two m2 (T. b. 211 and T. b. 580) from Taben buluk as aff. *Eumys*?. Lindsay (1977, p. 602) suggested that the four isolated teeth referred to *Cricetodon* and *Eumys* by Bohlin (1946) should be assigned to *Eucricetodon*. The two m2 are similar to the m2 from Lanzhou described

here. However, the characters of the m1 from Lanzhou, such as lacking anteroconid, protoconid and metaconid being subequal in size and opposite to each other in position, complete metalophid II and the form of the ectolophid, show that it belongs to the dipodid rather than cricetid.

Among the dipodids, the cheek teeth from Lanzhou are more similar to Allosminthus in having weakly developed mesolophid and more reduced posterior part of m3. They differ from Allosminthus in m2 having transverse metalophid, oblique mesolophid and lacking posterior arm of protoconid. They differ from Parasminthus, Plesiosminthus and Sinosminthus in the cheek teeth being wider and shorter, having simpler occlusal parttern, compressed cusps, better developed lophids, mesolophid short or even absent, m1 with higher metalophid II and metastylid, m2 with transverse metalophid, wide anterior fossettid and oblique ectolophid extending from protoconid to anterior arm of hypoconid, reduced m3 with fused hypolophid and posterolophid. The differences between the Lanzhou specimens and Heterosminthus and Protalactage are even more significant. It seems that they represent a new genus and species, which is named here Litodonomys huangheensis.

#### Sinosminthus sp.

(pl. II, 5)

One M1 (IVPP V 11774) from GL 9513C in Xiagou of Lanzhou Basin is similar to that of *S. inapertus* in having double metaloph, complete mesoloph, posteriorly oblique metaloph joining posteroloph, and symmetric sinus. It differs from *S. inapertus* in the main cusps and metaloph being slender and protocone having postero-lingual crest.

### 2 Discussion

# 2.1 The age of the lower red mudstone

The dipodids were collected from five localities of the lower red mudstone: GL 9513A, B, C of Xiagou and GL 9601A and B of Shangxigou, Lanzhou Basin. Stratigraphically all these five localities are situated in the middle part of the lower red mudstone. The dipodids include 8 species of 4 genera. Among them 4 species (*Parasminthus asiae centralis*, *P. tangingoli*, *P. parvulus*, and *Heterosminthus lanzhouensis* sp. nov.) are common to all the five localities and Taben buluk. As in Taben buluk, all the M1/2 of the three species of *Parasminthus* from Lanzhou has four roots. *Litodonomys huangheensis* gen. et sp. nov. found from GL 9513C and GL 9601B occurs also in Taben-buluk. It seems that the middle part of the lower red beds bearing the dipodids in Xiagou (GL 9513A, B, C) and Shangxigou (GL 9601A, B) of the Lanzhou Basin is equivalent to that of Taben-buluk in age. It is of late Oligocene.

# 2.2 The relationships among the Paleogene dipodids

**Character argumentation** The following analysis of the characters is based exclusively on the dentition. Major literature sources of data come from: Bohiln (1946), Green (1977), Hugueney & Vianey–Liaud (1980), Wang (1985), Huang (1992), Qiu (1996), and Tong (1997).

- 1) Mesoloph of M1/2: absent or weak (0), short (1), long (2);
- 2) Entoloph on M1/2: incomplete (0), complete (1);
- 3) Posterior concavity between hypocone and posteroloph on M1/2: absent (0), present but weak (1), well developed and with a lingual part of the posterior cingulum (2);
  - 4) Number of root on M1/2: three (0), three or four (1), four (2);
  - 5) Posterior arm of protocone on M1/2: absent or weak (0), well developed (1);
- 6) Anterior arm of protocone on M1: joining paracone (0), short and separated from paracone and parastyle (1), long and joining parastyle (2);
  - 7) Protoloph II on M1: absent (0), incomplete (1), complete (2);
- 8) Metaloph on M1: absent or weak (0), joining anterior arm of hypocone (1), joining hypocone (2), joining posterior arm of hypocone or posteroloph (3);
- 9) On M2 only protoloph I present (0), Protoloph I present and protoloph II variable (1), both protoloph I and II present (2), only protoloph II present, and anterior arm of protocone separated from paracone and extending antero-buccally (3);
- 10) Metaloph on M2: joining hypocone or its anterior arm (0), joining posterior arm of hypocone;
  - 11) Mesolophid on m1/2: absent or weak (0), middle (1), long(2);
- 12) Ectolophid on m1: weak or absent (0), complete and straight (1), complete and bend (2);
- 13) Ectolophid on m2: weak or absent (0), complete and joining protoconid (1), complete and joining posterior arm of protoconid (2);
- 14) Metalophid I on m2/3: weak or absent (0), complete, transverse and joining anterior arm of protoconid (1), complete, oblique anterobuccally and joining anteroconid;
  - 15) Hypolophid on m3: absent(0), present(1);
  - 16) Main cusps on molars: not alternate (0), alternate (1);
  - 17) Longitudinal groove on upper incisor: absent (0), present (1).

Phylogenetic analysis The terminal taxa are genera with the exception of Parasminthus, which is represented by three species (P. asiae-centralis, P. tangingoli and P. parvulus). We do not include Blentosomys dasikerkos, Aksyiromys dalos and Ulkenulastomys abrotos from the Obayla Svita in Zaysan Basin, which were referred by Shevyreva (1984) to ?Phiomyidae, or to family indet. of Myomorpha respectively,

0 0

0

0 ?

1 0

9

later to the Dipodidae by Mckenna and Bell (1997), because of the fragmentary nature of the specimens. Litodonomys is not included in our analysis because of its uncertain taxonomic position.

Taxa		Characters															
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Primisminthus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Banyuesminthus	ı	0	0	0	0	0	1	2	0	0	0	1	l	0	0	0	0
Allosminthus	ı	1	0	0	1	0	0	1	0	0	0	1	l	0	1	0	0
Sinosminthus	2	1	0	0	1	0	2	3	2	0	1	1	l	1	l	0	0
Heosminthus	2	1	0	0	1	1	2	2	ı	0	2	1	l	1	1	0	0
Plesiosminthus	2	1	0	0	1	2	2	2	1	0	2	1	l	1	1	0	1
Pa. parvulus*	2	1	0	1	1	2	2	2	0	0	2	1	1	1	ĺ	0	0
Pa. tangingoli*	2	1	ı	1	ı	2	2	3	2	0	2	1	ı	1	1	0	0

2

2 3

2 2 3 2

3

3

2

?

2 2 2 2 1 1 0

2

2 2

Table 4 Data Matrix of Paleogene dipodids (Question marks indicate missing data)

Pa. asiae-centralis

Gobiosminthus

Shamosminthus

Heterosminthus

Protalactaga

2

2

1

2

2

ŧ

2 2

2 2 1 2 2 3 3

2

Table 4 shows the data matrix of the Paleogene dipodids. A total of 13 taxa and 17 characters are used in calculation. The data were analyzed using the PAUP 3.1.1. Many of the characters have multistates (a total of 46 states). All characters are ordered and unweighted. The character optimization is applied using accelerated transformation (ACCETRAN). Branch and Bound search yielded two equal most parsimonious trees. Each tree has the following properties: tree length=38; consistency index (CI) = 0.789; Homoplasy index (HI) = 0.211; CI excluding uninformative characters = 0.778; HI excluding uninformative characters = 0.222; Rentention index (RI) = 0.857; Rescaled consistency index (RC) = 0.677. The two trees differ only in the positions of Shamosminthus and Protalactaga. The result of the phylogenetic analysis is shown in fig. 3.

The earliest known depodids may be Blentosomys dasikerkos, Aksyiromys dalos and *Ulkenulastomys abrotos* from the Obayla Svita. It is difficult to assess their relationships with other dipodids because they are based on single isolated teeth. As for the age of the Obayla Svita, it was suggested as early Eocene (Shevyreva, 1984; McKenna and Bell, 1997) or middle Eocene (Tong and Wang, 1981; Russell and Zhai, 1987). Based on the mammalian fauna from the Obayla Svita we agree with Tong and Wang (1981) in that the Obayla Svita may be equivalent to the Arshantan,

<sup>\*</sup> Pa. : Parasminthus

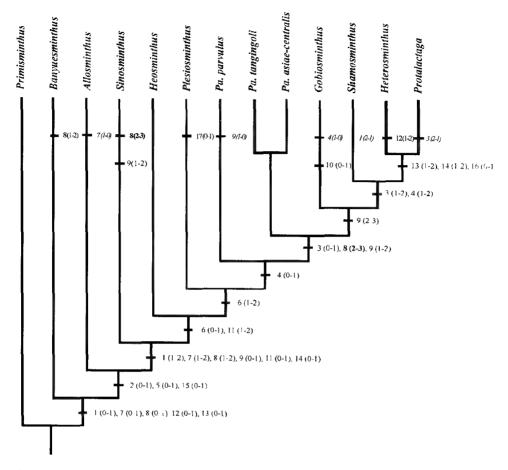


Fig.3 Cladogram of Paleogene dipodids generated by Branch and Bound search of PAUP 3.1.1

Pa.: Parasminthus; bold: parallel transformation; italic: reversed transformation

earlier than the Irdinmanhan, in age and is of early middle Eocene. Thus, the dipodids are known to appear first in the early middle Eocene.

Tong (1997) described three dipodid taxa from the Middle Eocene of Yuanqu Basin of Shanxi Province and Liguanqiao Basin of Henan Province in China: two new genera (*Primisminthus* and *Banyuesminthus*) and cf. *Sinosminthus* sp. It seems to us that *Primisminthus* represents the most primitive dipodid known. *Banyuesminthus* may form a sister group to other dipodids. As for cf. *Sinosminthus* sp., as mentioned by Tong (1997), it is quite different from *Sinosminthus* and its affinity with *Sinosminthus* is unclear.

Wang (1985) suggested that *Parasminthus* might be derived from some *Sinosminthus*-like forms. Tong (1997) thought that *Sinosminthus* was too advanced to be the ancestor of *Parasminthus*, because the metaloph of M1 of *Sinosminthus* joining the posteroloph or posterior arm of the hypocone might represent a more advanced

feature than that of some *Parasminthus*. In fact *P. parvulus* has this primitive feature as well. we agree with Tong (1995) that *Sinosminthus* may represent an early side branch of the dipodids. Having compared the late Eocene and Oligocene dipodids of Asia, we found that among the three taxa (*Sinosminthus*, *Allosminthus* and *Heosminthus*) of the late Eocene only *Heosminthus* may represent the main stalk and is the sister group to other later dipodids (including *Heterosminthus*, *Protalactaga* etc.).

Among the species of *Parasminthus* only *P. asiae-centralis*, *P. tangingoli* and *P. parvulus* are better known. As discussed above, the two formers are similar to each other in occlusal view, but the third species is different from the two formers. The cladistic analysis indicates that *P. parvulus* may form a sister group to *P. asiae centralis*, *P. tangingoli* and all the later dipodids. To include *P. parvulus* in the genus would inevitably make *Parasminthus* paraphyletic. However, it seems premature to establish a separate genus for *P. parvulus*, nor is it appropriate to combine it with *Heosminthus*.

As for the relationships of *Parasminthus* and *Plesiosminthus*, two major points of view were expressed. 1) *Parasminthus* is a valid genus (Bohlin, 1946, Engesser, 1979; Hugueney and Vianey Liaud, 1980; Wang, 1985 and Huang, 1992). 2) *Parasminthus* and *Plesiosminthus* should be combined into one genus, *Plesiosminthus* (Stehlin and Schaub, 1951; Wilson, 1960; Shevyreva, 1970; Kowalski, 1974, p. 168; Lindsay, 1977 and Li and Qiu, 1980). McKenna and Bell (1997) further lumped *Schaubeumys*, *Heosminthus*, *Parasminthus*, *Sinosminthus*, *Shamosminthus* and *Gobiosminthus* into one genus *Plesiosminthus*. Green (1977, 1992) thought *Schaubeumys* is a junior synonym of *Pleisiosminthus*. As for the other genera, as the cladistic analysis shows (fig. 3), *Plesiosminthus* would be a highly polyphyletic taxon if we lump all the genera mentioned above into this genus.

Qiu et al. (1981) supposed that Protalactaga might have derived from Parasminthus (P. tangingoli). Qiu (1996) suggested two lineages in the dipodids: Parasminthus (P. parvulus) - Heterosminthus - Lophocricetus, and Parasminthus (P. asiae-centralis) - Protalactaga - Allactaga. The Lanzhou specimens show that Heterosminthus lanzhouensis may represent the transitional stage Parasminthus to from Heterosminthus orientalis. derive Heterosminthus may from the lineage Parasminthus (P. tangingoli) which has a long posterior arm of protoconid on m2. Likewise, Protalactage may derive from Parasminthus with mesolophid, by posteriorly shifting of mesolophid in m2. It means that both Heterosminthus and Protalactaga can derive from the same group near Parasminthus tangingoli.

There are two major points of view as to the higher classification of the Dipodidae: 1) Zapodidae is separated from the Dipodidae as a family (Simpson, 1945; Wood, 1955; Schaub, 1958; Wang, 1985; Martin, 1994; Qiu, 1996; Tong, 1997); 2)

They belong to one family Dipodidae (Ellerman, 1940; Hugueney & Vianey Liaud, 1980; McKenna & Bell, 1997). In the first case either *Parasminthus* and *Heterosminthus* are assigned to the Zapodidae, while *Protalactaga* and *Allactaga* to the Dipodidae (Simpson, 1945; Wood, 1955; Martin, 1994; Qiu, 1996), or only *Parasminthus* is assigned to Zapodidae, and *Heterosminthus*, *Protalactaga* and *Allactaga* to the Dipodidae (Schaub, 1958). It seems to us more reasonable to include all *Parasminthus*, *Heterosminthus*, *Protalactaga* and *Allactaga* in one family, the Dipodidae, if both *Heterosminthus* and *Protalactaga* originated from the group near *Parasminthus tangingoli*.

Originated from Asia in the early middle Eocene (or earlier?), the dipodids diversified rapidly. *Primisminthus* may represent a primitive lineage ranging through middle to late Eocene. *Banyuesminthus* is the sister group to other depodids. In late Eocene *Allosminthus* and *Sinosminthus* may represent two side lineages and *Heosminthus* may represent the main stem and forms a sister group to the other later dipodids. The latter lineage ranges from late Eocene through late Oligocene. In Oligocene this lineage diversified into several branches. One branch represented by *Plesiosminthus* migrated into Europe, and then into North America. Another branch remained in Asia, where it evolved from *Parasminthus* into five lineages: the genus *Parasminthus* itself survived until middle Miocene; *Gobiosminthus* and *Shamosminthus* represent two side lineages; the fourth one evolved into *Heterosminthus Lophocricetus* etc; the fifth one developed into *Protalactaga Allactaga* etc.

The living dipodids are the animals well adapted to the drier grassland or savanna habitat in the Holarctic Region. Their rich occurrence in Lanzhou Basin shows that the paleoclimatic condition of late Oligocene of the Lanzhou area might already be rather dry, similar to that of the recent time of this area.

# 3 Conclusion

- 1) Eight species of four genera of the dipodids are discovered in the red mudstone of the Lower Member of the Xianshuihe Formation. The Lanzhou material shows that *Parasminthus asiae centralis*, *P. tangingoli* and *P. parvulus* are stable in features in late Oligocene. Those from Ulantatal area represent affinis species of the three species.
- 2) Originated from Asia in early middle Eocene (or earlier), the dipodids diversified rapidly. *Parasminthus*, one of the most abundant and flourishing rodents in mid-Tertiary in Asia, represents an important evolutionary stage in dipodid history.
- 3) The middle part of the lower red mudstone in Xiagou and Shanxigou in the Lanzhou Basin is of late Oligocene in age.
  - 4) At least during the late Oligocene the Lanzhou area might have established

grassland or savanna habitat, where the dipodids highly diversified and became one of the more flourishing rodents.

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# 图版说明 (Explanations of plates) 图版 I (Plate I)

副蹶鼠颊齿冠面(Occlusal view of cheek teeth of Parasminthus)

1~8. 党河副蹶鼠 *P. tangingoli* Bohlin, 1946: 1. 右(right) P4 (V 11753.1), 2. 左(left) M1 (V 11753.3), 3. 左(left) M2 (V 11753.4), 4. 右(right) M3 (V 11753.9), 5. 左(left) M3 (V 11755.8), 6. 右(right) m1 (V 11753.10), 7. 左(left) m2 (V 11753.12), 8. 右(right) m3 (V 11753.14);

9~14. 中亚副蹶鼠 *P. asiae centralis* Bohlin, 1946: 9. 右(right) P4 (V 11750.1), 10. 右(right) M1 (V11750.2), 11. 左(left) M2 (V 11750.3), 12. 左(left) m1 (V 11750.4), 13. 左(left) m1(V 11748.1); 14. 右(right) m2 (V 11748.5)

标尺 (scale bar) = 1mm

### 图版 II (Plate II)

- 1~4. 小鼠蹶鼠 Parasminthus parvulus Bohlin, 1946: 1. 右上颌具 P4~M1 腹面 (ventral view of right upper jaw with P4~M1, V 11758.1), 2. 左M1~2 冠面 (occlusal view of left M1~2, V 11758.2), 3. 右M3 冠面 (occlusal view of right M3, V 11758.73), 4. 左下颌具 m1~3 冠面 (occlusal view of left lower jaw with m1~3, V 11759.66);
- 5. 中华蹶鼠未定种 Sinosminthus sp. 左 M1 冠面 (occlusal view of left M1, V 11774);
- 6. 副蹶鼠未定种 Parasminthus sp.II 右 M1 冠面(occlusal view of right M1, V 11766.1);
- 7. 中亚副蹶鼠 Parasminthus asiae-centralis Bohlm, 1946 左 m3 冠面(occlusal view of left m3, V 11749.4);

8. 副蹶鼠未定种 *Parasminthus* sp.I 左 m2 冠面(occlusal view of left m2, V 11765) 标尺(scale bar) = 1mm (Figs.1~7 share one scale bar and fig.8 has its own scale bar)

#### 图版 III(Plate III)

1~8. 兰州异蹶鼠(新种) Heterosminthus lanzhouensis sp. nov. 颊齿冠面(occlusal view of cheek teeth): 1. 左(left) M1 (V 11772.1), 2. 左(left) M2 (V 11771.1), 3. 左(left) M2 (V 11772.2), 4. 右(right) M2 (V 11771.2), 5. 左(left) m1 正型标本(holotype, V 11773.1), 6. 右(right) m1 (V 11771.3), 7. 右(right) m2 (V 11769.2), 8. 右(right) m2 (V 11773.8);

9~12. 黄河简齿鼠 (新属新种) *Litodonomys huangheensis* gen. et sp. nov., 颊齿冠面 (occlusal view of cheek teeth): 9. 右 (right) ml (V 11768.2), 10. 右 (right) m2 正型标本 (holotype, V 11768.1), 11. 左 (left) m2 (V 11768.3), 12. 右 (right) m3 (V 11767.2)

标尺(scale bar) = 1mm

